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Substitution of winter chilling by spring forcing for flowering using sweet cherry as model crop



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ABSTRACT

Many horticultural crops such as apple, pear, plum, cherry, strawberry and Asparagus require a cold period in winter (chilling) with a subsequent warm period (forcing) for flowering. The objective of the present work was to investigate the effects of more forcing due to projected diminishing available chill as a result of climate change and elaborate the possibility of substitution of chilling by forcing, using cherry as the most affected crop. Therefore, 160 potted sweet cherry trees were exposed to different chilling in four consecutive winters at Klein Altendorf, near Bonn ($50\,^{\circ}$ N), Germany. Three cherry cultivars with a wide range of chilling requirement (3-fold) were employed in eight scenarios per variety per year, ranging from -50% less/insufficient chill for warm temperature zone winters to +50% more or excess chill for cold winter fruit growing regions:

- 1. The *minimum chill* fulfilment of the cherry trees ranged from 400 CH (Chilling Hours) in low chill, 550 CH in medium chill and 750 CH in the high chill variety associated with *maximum forcing* of ca. 11.000 GDH (Growing Degree Hours) for low, ca. 12.000 GDH for medium and ca. 13.000 GDH for high chill varieties for sufficient flowering.
- 2. With *optimum* chill, the *optimum* forcing was ca. 8.000 GDH (> 12 °C), irrespective of variety, allowing upscaling of the results to possibly other varieties. Trees exposed to *excess chilling* (150%) required less forcing (ca. 4000 GDH) to reach full bloom. Hence, chilling can compensate for up to half of the required forcing, i.e. ca 4.000 GDH.
 - 3. Ratios of forcing to chilling were computed for future comparisons, which ensure flowering in the orchard.
- 4. Slightly negative temperatures (-5 °C to 0 °C), which are presently exempt in the common chilling models but common in the fruit growing regions, contributed to chilling accumulation of the fruit trees.
 - 5. A novel scheme was developed to visualise these regulatory mechanisms in tree physiology.

Overall, the results have shown that diminishing chilling as a result of climate change can be compensated for, in part up to 50%, by a larger amount of forcing to obtain natural flowering in the orchard.

1. Introduction

Many horticultural crops such as apple, pear, plum and cherry, as well as strawberries and perennial vegetables such as *Asparagus* require chill, i.e. a period of cool temperature during the winter season to induce buds to flower in spring (Lang et al., 1987). Winter temperatures differ from the colder Scandinavian climate to the Mediterranean climate, the latter associated with possibly insufficient winter chilling (cold period) followed by a longer period of forcing. Climatic conditions in temperate zones, where cherry is grown, as an intermediate situation are characterized by variable winter chilling followed by a forcing period (Couvillon and Erez, 1985); recent climate change may reduce available chilling in temperate zones (IPCC, 2013). In the past, the

emphasis of studies was on chilling, whereas the subsequent forcing received relative little attention. Hence, it remains unclear, whether shorter or longer chilling periods in the winter can be compensated or substituted, and to which extent, by longer or shorter forcing periods, to ensure flowering and hence yields in the orchard.

Among fruit crops, sweet cherry (*Prunus avium* L.) requires the greatest chilling with up to 1500 Chilling Hours (CH) (Kaufmann and Blanke, 2017a), which is hence categorised as one of the most affected tree crop by environmental change and consequent temperature rises, particularly in warmer winters (Luedeling et al., 2011a) and was chosen here as model crop. In Southern France, mild winters with insufficient chilling led to an average of 32% yield loss in sweet cherry (Millan et al., 2009). The relative portions of forcing and chilling requirements

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are difficult to quantify due to uncertainty of a number of issues. Past chilling experiments with cut branches in moist paper in the dark at a constant temperature in a cold chamber (Mahmood et al., 2000a; Heide, 1993; Alburquerque et al., 2008; Ramos et al., 2018) allow relatively easy quantification of chill effects, but conclusions drawn from such artificial environments are difficult to apply to whole trees under natural weather and light viz. environmental conditions (photoperiod) (Mahmood et al., 2000b). To our knowledge, no study has been carried out with in-situ observations (over several years) on (potted viz. transportable) entire intact cherry trees of different varieties with a broad range of chilling requirement and exposed to 24 scenarios (different chilling and forcing conditions) each winter including natural winter temperature regimes and modified environmental conditions in an unheated greenhouse to simulate climate change.

The hypothesis of this work was that chilling and forcing can be substituted by each other to a certain extent and one can compensate for the other, irrespective of variety, a result, which can be used in upscaling and that negative temperatures contribute to chilling accumulation.

The objective of this project was to investigate the effect of diminishing available chill as a result of climate change on forcing accumulation. This study further aims to elaborate thresholds for minimum chilling fulfilment and its interaction with forcing accumulation. The work includes possible effects of slightly negative temperatures (0 °C to $-5\,^\circ\text{C}$) and the effects of simulated climate change with a predicted 2 °C global temperature increase (IPCC, 2013) on chilling availability in the temperate climate zone (50 °N), the major pome and stone fruit growing belt in Europe using climate sensitive sweet cherry as model crop. To achieve these goals, 160 potted sweet cherry trees of three varieties with a wide range of chilling requirements were raised over two years to initiate uniform flower buds before applying 24 chilling scenarios (8 scenarios per variety) per year followed by forcing to determine the effect on flowering.

2. Materials and methods

2.1. Location and environmental conditions

Klein-Altendorf Research Centre is located near Bonn, Germany (50 °N) with an averaged 9.8 °C annual temperature and a mild Westerly wind climate buffered by the Rhine valley during the winter (Blanke and Kunz, 2009). Chilling accumulated in winters 2012/13, 2013/14, 2014/15 and 2015/16 either outside in the orchard or in an unheated greenhouse to simulate recent climate change at Campus Klein-Altendorf of the University of Bonn (Table 1).

2.2. Materials - sweet cherry trees

The 160 sweet cherry (*Prunus avium* L.) trees (colour supplement 1) were grafted on dwarfing GiSelA 5 rootstock and planted in 35 L pots on 24 March 2011 in order to initiate uniform flower buds over the 1.5

Table 1 Average (based on hourly records) temperatures in the orchard and unheated greenhouse during the chilling period in the winter.

Date	Location	Winter temperature in ${^{\circ}C}^{^{\ast}}$
Winter 2012/13	Orchard	3.4
	Unheated Greenhouse	4.7
Winter 2013/14	Orchard	6.0
	Unheated Greenhouse	7.0
Winter 2014/15	Orchard	4.7
	Unheated Greenhouse	6.8
Winter 2015/16	Orchard	6.7
	Unheated Greenhouse	8.2

^{* 22} October till 28 February.

years before chilling treatments commenced in October 2012. The sweet cherry varieties were chosen to cover their widest possible range in chilling needs, a high chill variety 'Schneiders späte Knorpelkirsche', 'Brooks' as a medium chill and '6000CZ' as a low chill variety (Gratacós and Cortés, 2007; Luedeling et al., 2013; Kaufmann and Blanke, 2017b). The cv. 'Schneiders späte Knorpelkirsche' is an old widespread variety and first archived in 1850 in Europe, while both cvs 'Brooks' and '6000CZ' are from California, the latter especially bred for its low chilling environment.

2.3. Methods - experimental layout and scenario description

Eight groups of four trees were formed for each variety. To acquire chilling, trees of the first three groups of each variety were placed in an unheated greenhouse in the autumn, while those of the second three groups were left outside in a cherry orchard. For these two groups, viz. unheated greenhouse and orchard, a control group with four trees of each variety was set up under the two environments. Each group of four trees equals one climate scenario; a certain amount of natural accumulated chilling and forcing in a heated greenhouse.

Chilling was assessed using beginning of leaf fall as physiological plant parameter (Kaufmann and Blanke, 2017b) with intact potted trees subjected to one of eight climate scenarios (Table 2) under natural conditions in terms of diurnal temperature and photoperiod fluctuations; this is in contrast to previous reports with cut branches stored in a refrigerator at a constant temperature without light. Our scenarios included exposure to either about 50% less chilling of the estimated chilling optimum, or up to 50% additional chilling on top of the chilling optimum to cater for all possible weather extremes, possibly associated with environmental change and areas of increased chill projection.

After the targeted chill accumulation was reached, the potted trees were transported from the orchard or the unheated greenhouse to a heated greenhouse with the natural photoperiod and diurnal temperature fluctuation (heated to $> 12\,^{\circ}$ C) to prevent any further chilling and subject the cherry trees to environmental conditions to start forcing and induce flowering. In the heated greenhouse, flower buds were counted on each tree and full bloom assessed, when 50% of flowers for a tree opened (BBCH 65; Meier et al., 1994 equivalent to F2; Fleckinger, 1955). Groups viz scenarios are labelled as follows. The first letter of the scenario abbreviation denotes the cherry variety (C= '6000CZ'; B='Brooks'; S='Schneiders'), the first number the year (2012/13 = 1... 2015/16 = 4), the second the letter location (orchard = O, unheated greenhouse = G) and last number the group in each year (Table 2).

2.4. Computation of the three chilling models based on our own hourly temperature records

Chilling Hours, Units and Portions were computed from our own onsite meteorological data obtained at 10 min intervals from temperature loggers (Datahog, Skye Ltd., Pontys, Wales, UK) placed at 2 m height between the trees. Chilling computation started at the beginning of leaf fall, the period identified when the tree prepares for dormancy (Hillmann et al., 2016; Kaufmann and Blanke, 2017b) (Table 2). Chilling was computed using the Utah model, the Dynamic model and the Growing Degree Hours with the program "R" ("R" version 2.15.3, Lucent Technologies, USA) and R-chill package (Luedeling et al., 2011b). In the computation, we used the oldest and most widespread Chilling Hours model, which adds the number of hours with temperatures of 0 to 7.2 °C (Weinberger, 1950). It was originally developed for peaches in Georgia (USA), but is now applied to many other types of fruit crops in other climates without adaption. Since the Chilling Hour model originated from warm winter regions without frost, we computed two versions of the Chilling Hour model, the original approach (Weinberger, 1950) and our own modified version for an environment with slightly negative temperatures (-5 °C to 7.2 °C), typical for the temperate zone fruit growing belt along 50 °N. The third chilling model applied was the

 Table 2

 Sweet cherry varieties employed in the present experiment, their origin, chilling estimates, treatment (chilling exposure), treatment designation and time of leaf drop.

Variety	Origin (country)	Environment (winter climate) at origin	Alleged chilling hours (CH)	Chilling applied in experiment (scenarios)	Begin leaf fall in 2012 till 2015
'6000 CZ'	California, USA	Mild maritime med	ca. 500 CH	250 CH up to 800 CH (C2O2; C2G2)	30 October 2012 25 October 2013 03October 2014 22 October 2015
'Brooks'	California, USA	Mild maritime med	411.5 CH*, 720 CH**	400 CH up to 1400 CH (B2O2: B2G2)	14 October 2012 16 October 2013 01 October 2014 20 October 2015
'Schneiders späte Knorpelkirsche'	Germany	Cold Continental	ca. 1400 CH***	800 CH, up to 2000 CH (S2O2; S2G2)	20 October 2012 23 October 2013 08 September 2014 16 October 2015

- * Alburquerque et al., 2008.
- ** Gratacós and Cortés, 2007.
- *** Luedeling et al., 2013.

Utah model, also developed for peaches in Utah (Richardson et al., 1974), in which temperatures are weighted and especially warm temperatures can nullify already accumulated chilling. In the Utah model, effective chilling temperatures range from 1.4 °C to 12.4 °C and temperatures above 15.9 °C can overcome previous chilling effects. The Dynamic Model (Fishman et al., 1987; Erez et al., 1990) was also developed for peaches in Israel. It divides the chilling in a two-phase process. In the first phase, cold winter temperatures lead to a precursor of the chilling accumulation. This precursor is "vulnerable" and can either be negated by warm temperatures or taken into account (realized) as one Chill Portion (CP) by cool temperatures. These Chill Portions will then remain until the end of the winter. Physiologically, this model (CP) is based more on speculation rather than biological facts, but in comparison to the other models it seems to be plausible.

2.5. Forcing- using GDH

Once trees reached our pre-set chilling target, we transported the potted cherry trees to a greenhouse heated to $> 12\,^\circ\text{C}$ to start forcing; forcing progress was computed based on the Growing Degree Hours (GDH) model by Anderson et al. (1986), with a base temperature of 4 $^\circ\text{C}$ and maximum temperature of 36 $^\circ\text{C}$ with a maximum effective point of 25 $^\circ\text{C}$ until 50% flowers of a tree opened. Trees, which had not flowered or abandoned their flower buds during 24,000 GDH of forcing, were categorised as not fulfilled their chilling requirement.

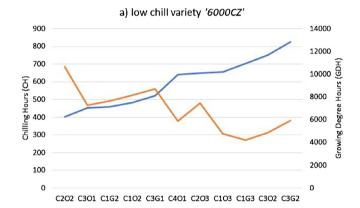
3. Results

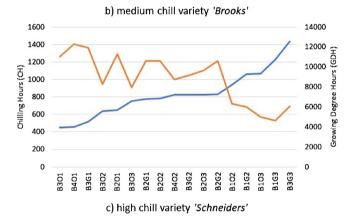
The first objective of this present work was to investigate, to which extent forcing can compensate for chilling and vice versa and elaborate thresholds for minimum chilling fulfilment for natural flowering.

3.1. Interchangeability of chilling and forcing

Fig. 1 shows 19 scenarios of winter chill, expressed as Chilling Hours (CH), versus forcing expressed as Growing Degree Hours (GDH), based on trials over four consecutive winters and three (low, medium and high chill) varieties. In the experiment, potted cherry trees had been kept either under natural environmental viz. winter conditions at 50 °N or in an unheated greenhouse (to simulate climate change) with natural day night light cycle. After the intended chilling accumulation, the trees were transported to a heated greenhouse to cease further chilling and start the forcing phase.

Fig. 1 includes up 19 scenarios of different chilling to forcing relationships starting from 50% less chilling up to 50% more chilling than required by each variety. The blue curves for chilling accumulation in Fig. 1 start with excess chilling (+50%) of the respective chilling needs and the lowest forcing at a minimum of ca. 4000 GDH, irrespective of variety, to reach full bloom (Fig. 1). As trees had been exposed to less chilling, e.g. by earlier removal from the orchard or from the unheated





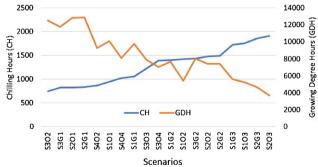


Fig. 1. Chilling and forcing scenarios (from winter 2012/13 till 2015/16) of a) low, b) medium and c) high chill cherry varieties in ascending chilling accumulation (scenarios with insufficient chilling did not reach flowering and are hence not shown).

greenhouse, their forcing requirement increased to reach full bloom. Minimum chill fulfilment ranged from 400 CH in the low chill, 550 CH in the medium chill and 750 CH in the high chill variety to reach full

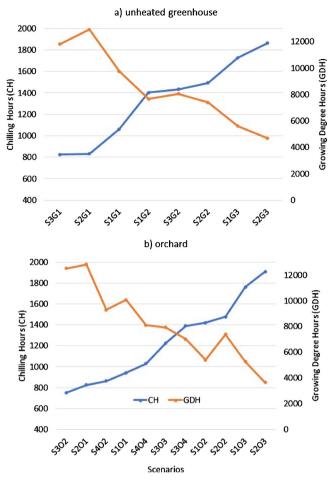


Fig. 2. Chilling and forcing of sweet cherry cv. 'Schneiders späte Knorpelkirsche' in a) an unheated greenhouse (to simulate climate change) and the b) orchard over four consecutive winters from 2012 until 2016 in ascending chilling accumulation.

bloom. As a result, forcing increased from ca. 4000 GDH to 11,000 GDH for low chill, 12,000 GDH for medium chill and to 13,000 GDH for high chill varieties to reach full bloom. In all these cases, the intersection of the chilling and the forcing curves in Fig. 1 was between 7,000–8,000 GDH, irrespective of the variety.

3.2. Partial substitution of insufficient chilling by forcing between orchard and greenhouse

Trees in their natural environment in the orchard and in the unheated greenhouse (simulated climate change) showed commensurate courses in their chilling and forcing accumulation. Sweet cherry cv. 'Schneiders späte Knorpelkirsche' was chosen as typical representative starting at the scenario of ca. +50% excess chill (1900 CH) to -50%less or lack of chilling (750-800 CH) (Fig. 2). Optimum chilling was fulfilled at about 1400 CH and about 8000 GDH until 'Schneiders' reached full bloom, irrespective of environment (orchard or unheated greenhouse), where these temperatures were accumulated. The response curve of trees placed in an unheated greenhouse followed a more linear path of chilling and forcing due to fewer temperature fluctuations; both environments provided a minimum of ca. 800 CH chilling; any missing chill above 800 CH was compensated by forcing of 13,000 GDH or less to reach full bloom (Fig. 2). By contrast, excessive chilling of ca. 1900 CH combined with lesser forcing of between 4500 GDH in the unheated greenhouse (Fig. 2a) and about 3500 GDH in the orchard (Fig. 2b) provided natural flowering. This discrepancy in forcing velocity could result from a greater portion of chilling below 0 °C

Table 3Forcing to chilling ratios for optimum and minimum flowering.

Ratio of Growing Degree Hours to	High chill variety	Medium chill variety	<i>Low</i> chill variety				
Optimum forcing to chilling ratios for optimum flowering							
Chilling Hours & Chill Units	5	10	15				
Chill Portions	100	200	300				
Minimum forcing to chilling ratios for flowering							
Chilling Hours & Chill Units	15	20	25				
Chill Portions	200	300	400				

(Example for high chill varieties: with 7500 GDH forcing and 1500 CH chilling results in the optimum flowering ratio of 5 whereas 12,000 GDH forcing and 800 CH chilling result in minimum flowering ratio of 15; ratios in excess of 15 prohibit flowering).

accumulated in the orchard, which is not accounted for in the three chilling models.

3.3. Ratios of forcing to chilling for natural flowering

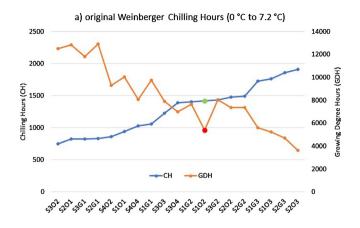
In order to determine the environmental conditions required for natural flowering, the forcing to chilling ratios were computed from the chilling data in Fig. 1; synchronous flowering of a tree and trees in the orchard is required for successful pollination. Ratios of forcing (Growing Degree Hours; GDH) to Chilling Hours (CH) or Chill Units (CU) of greater than 15:1 for high chill varieties, 20:1 for medium chill varieties and 25:1 for low chill varieties were an indicator of retarded or sporadic flowering. Overall, 25 times more forcing hours (e.g. 10,645 GDH) than Chilling Hours (e.g. 402 CH) are required for natural flowering in scenario C2O2 (Fig. 1). With Chilling Portions this is equivalent to GDH to Chill Portions (CP) ratios greater than 200:1 for high chill varieties, greater than 300:1 for medium chill varieties and greater than 400:1 GDH to CP for low chill varieties (Table 3). Optimum chilling with natural flowering was found, when forcing (GDH) to chilling (CH or CU) ratios are lower than 5:1 or GDH to CP lower than 100:1 for high chill varieties. For medium chill varieties, GDH to CH or CU ratios were lower than 10:1 or GDH to CP was lower than 200:1: for low chill varieties ratios of GDH to CH or CU were lower than 15:1 or GDH to CP was lower than 300:1 to obtain natural flowering in the cherry trees (Table 3).

3.4. Influence of slightly negative temperatures (0 °C to -5 °C)

The conspicuous trough in Fig. 3a can be explained by the different computing approaches: The original Weinberger Chilling Hour model produced a conspicuous trough in forcing marked red associated with the respective chilling value marked in green. In our modified Weinberger version we included slightly negative temperatures; trees in this scenario S1O2 consequently accumulated over 30% more chilling (2113 CH- vs 1421 CH) (Fig. 3). However, both approaches interestingly resulted in the same amount of forcing of 5405 GDH for flowering. This result is interpreted in a way that slightly negative temperatures may contribute to chilling of a tree, however, to a lesser extent than slightly positive temperatures. By comparison, winters without negative temperatures, cherry trees with 1400 CH needed about ca. 7500 GDH of forcing.

4. Discussion

The overall objectives of the present study were to elaborate, whether forcing can partially substitute for lack of chilling (and to which extent) and whether slightly negative temperatures down to $-5\,^{\circ}\text{C}$ can contribute to chilling accumulation for sustainable fruit production in the future. The results have shown forcing to chilling



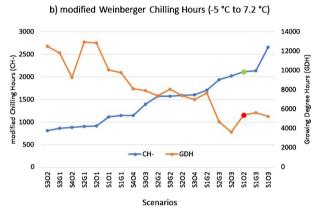


Fig. 3. Comparison of a) the original Chilling Hour model (Weinberger, 1950) and b) our modified version including slightly negative temperatures (0 to $-5\,^\circ$ C). Green (chilling) and red (forcing) dots denote values in scenario S1O2, in which cherry trees received 1421 Chilling Hours (above 0 °C) and 2113 modified Chilling Hours (including negative temperatures down to $-5\,^\circ$ C), respectively and 5,405 Growing Degree Hours forcing (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

ratios of 5:1–15:1 for flowering in high chill varieties and in the light of recent climate change that up to 50% of chilling can be substituted by additional forcing viz a longer forcing period and slightly negative temperatures (-5 °C to 0 °C) contribute to chilling fulfilment and have to be included in the chilling period.

4.1. Interchangeability of chilling and forcing

Our results (Fig. 1) showed that a minimum chilling is required before forcing can become effective, a finding, which is in contrast to the 'Parallel model' (Landsberg, 1974), who assumed that both chilling and forcing accumulation start parallel at leaf fall. Changes in carbohydrates in the buds during dormancy were assessed (Chmielewski et al., 2017; Kaufmann and Blanke, 2017c) indicating a minimum chilling requirement has to be fulfilled before forcing accumulation enable the bud to flower (Fig. 4). Genetic studies on dormancy indicate that a minimum chill accumulation must be met first before heat accumulation can enable the expression of DAM genes that result in the promotion of flowering (Horvath, 2009; Leida et al., 2012

Our approach also differs from that of Pope et al. (2014) and the more theoretical overlap model developed in the warm winter climate of California, USA. Our approach is based on the finding of the optimal forcing of 8000 GDH, irrespective of cultivar (low, medium, high chill), irrespective of scenario (-50% to +50% chilling) and chilling model. These results from 24 scenarios with portable intact cherry trees clearly

of very different chilling requirement enable to distinguish between actual chilling due to temperate climate zone winters and forcing in a heated greenhouse. The basis of this threshold of 8000 GDH of forcing maybe a useful requisite for horticulturists to calculate and predict effects of insufficient chilling e.g. in the Mediterranean and excessive chilling in e.g. Scandinavia. For cherry, up to 50% of chilling may be compensated by forcing (in the scenario with the lowest chill accumulation with sufficient flowering) and vice versa. This may enable a comparison of cherry and other fruit crops as their suitability of cultivation in a particular location and possibly predict flowering. If more than 8000 GDH are needed for full bloom, chilling availability at this growing location declines for those varieties and vice versa.

Our results have shown that up to 50% of chilling can be substituted by additional forcing (Fig. 3/Table 3), i.e. exposure of the trees to longer spells of warm temperatures. This finding is in line with Couvillon and Erez (1985), who were probably the first to suggest such an idea for fruit species grown in Georgia, Athens, USA, but without designating ratios to the different species in relation to their chilling requirement (based on cut branches and concluding that bud break is determined by chilling requirement and not forcing accumulation). This finding of chilling substitution is relevant in the context of recent climate changes like warmer winter temperatures (IPCC, 2013) with a projected decline in available chilling in Europe (Luedeling et al., 2011a). As a result of climate change, bloom time of deciduous fruit trees is advanced by 6-10 days (Legave et al., 2012; Chmielewski and Rötzer, 2001; Cleland et al., 2007). In the past, most studies focused on the chilling period (Cesaraccio et al., 2004; Erez et al., 1990; Luedeling et al., 2011b; Luedeling, 2012) or rarely included forcing and then ended their observations as early as the green tip without waiting for the outmost chilling success, the flower (Alburquerque et al., 2008; Campoy et al., 2011; Marra et al., 2002). In Norway, a cold winter environment with sufficient chilling, and comparable to our 'excess chilling scenarios', only GDH (ca 4.000) are used for the prediction of flowering of sweet cherry (Meland et al., 2017), which compares favourably with our forcing values (3,500-4,000 GDH) with excessive chilling accumulation under our temperate zone climate (Fig. 1).

4.2. Effect of simulated climate change on chilling in the orchard and unheated greenhouse

In our experiment, the temperature in the unheated greenhouse exceeded that in the natural environment (orchard) by ca. 2 °C (Table 1) to simulate climate change. Although chilling and forcing values were similar in both locations, trees in the unheated greenhouse (climate change scenario) reached their chilling earlier than those outside in the field due to the rise in winter greenhouse temperature. Chilling built up faster in the beginning of dormancy in the orchard due to buffered temperature in the unheated greenhouse. During winter, the situation reverses and chilling accumulated faster in the unheated greenhouse due to fewer temperature drops below 0 °C, without chilling effect in the chilling models (Weinberger, 1950; Richardson et al., 1974; Erez et al., 1990). This finding enables the proposed forcing and chilling interaction possibly applicable to other locations within the temperate zone winters. Due to warmer spring temperatures in the unheated greenhouse, the full bloom of control trees was enhanced by about 7–12 days depending on year and variety. To our knowledge, this has not been investigated before so further discussion does not apply.

4.3. Ratios of chilling to forcing for sufficient flowering

As a result of the chilling and forcing values obtained from the different scenarios in our experiments (Fig. 1), the minimum value for flowering for the ratio of forcing (GDH) to chilling (e.g. CH) is visualized in a graphical abstract (Fig. 5). To our knowledge, this is the first time that ratios of GDH to CH/CU/CP for (in-) sufficient flowering and forcing values were established for the fruit crop most affected by

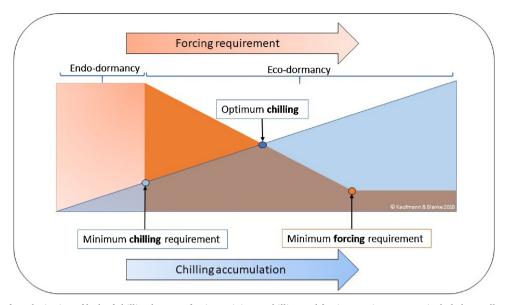


Fig. 4. General scheme for substitution of lack of chilling by more forcing. Minimum chilling and forcing requirements are included as well as the optimum chilling, irrespective of species and cultivar.

climate change, sweet cherry (Kaufmann and Blanke, 2017a), irrespective of their chilling requirement. Since a comparable visualization has not been published to our knowledge, discussion does not apply.

4.4. Influence of slightly negative temperatures (0 $^{\circ}\text{C}$ to $-5\,^{\circ}\text{C})$ on winter chill

The three most common chilling models ignore temperatures below 0 °C and may result from their warm winter origin. In the temperate climate zone, where many fruit trees are grown, winters may exhibit temperatures below zero. Trees therefore adapted to these temperatures like "Schneiders späte Knorpelkirsche", which is grown from warm winter climates in Turkey (under its synonym 'Ziraat'), where chilling requirements are hard to fulfil, up to Norway with constant freezing temperatures during winter. Although Mahmood et al. (2000a) had already suggested that slightly negative temperatures of -1.2 °C down to -5.6 °C might have an effect of overcoming dormancy, his experiments with cut one-year-old sweet cherry shoots from two-year-old trees held in a fridge at constant -1.2 °C in the dark to overcome dormancy ended before flowering and without calculating the required

forcing.

Our results with fully-grown, intact trees show that sub-zero temperatures in the winter may have an effect on chilling and dormancy breaking in line with Mahmood et al. (2000a and b) expectation. The successful result is seen in the example of our modified Weinberger Chilling Hours version including slightly negative temperatures (Fig. 3b) vs. the original Weinberger Chilling Hours model (Fig. 3a), trees in this scenario S1O2 consequently accumulated over 30% more chilling (2113 CH- vs 1421 CH). However both approaches interestingly resulted in the same amount of forcing (5405 GDH). This result is interpreted in a way that slightly negative temperatures contribute to chilling of a tree, however to a lesser extent than slightly positive temperatures. In winters without negative temperatures, trees with 1400 CH needed about ca. 7500 GDH of forcing.

5. Conclusions

Warmer winters as a result of climate change (IPCC, 2013) require adaption strategies in horticulture (Bindi and Olesen, 2011; Bisbis et al., 2018), including those to overcome the lack of chilling. Since cherry is

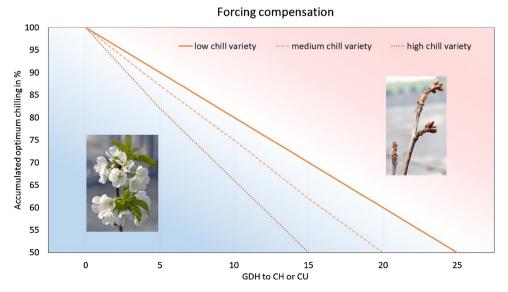


Fig. 5. Forcing can successfully compensate inadequate chilling levels at 50-100% of optimal chilling at ratios GDH to CH or CU of < 15:1 for high chill varieties, < 20:1 for medium chill varieties and < 25:1 with low chill varieties; the top right hand corner symbolises inadequate chilling and no flowering (the trees did not reach full bloom > 50% flowering), whereas the left bottom corner represents sufficient chilling and forcing, which lead to optimum flowering.

one of the most affected fruit crop by climate change (Luedeling et al., 2011a; Kaufmann and Blanke, 2017a) the thresholds, ratios and optimum forcing values presented in this study may also help growers and breeders to combat upcoming environmental changes. The interchangeability of chilling and forcing may also help to compare and explain varying chilling values determined in different regions (warmer or colder winters) for the same cultivar.

Acknowledgement

We are grateful to the local cherry growers association for funding the original 160 potted cherry trees, to Achim Kunz and Karl J. Wiesel for cultivating the cherry trees in pots over several years at Klein Altendorf, Professor Eike Luedeling for computing support of the models and Professor Georg Noga, University of Bonn and DLR Klein-Altendorf for supporting this project.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: https://doi.org/10.1016/j.scienta.2018.09.021.

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